North American Journal of Fisheries Management

ISSN: 0275-5947 print / 1548-8675 online
DOI: 10.1002/nafm.10254

ARTICLE

Performance of Diploid and Triploid Westslope Cutthroat Trout Fry Stocked into Idaho Alpine Lakes

John D. Cassinelli
Idaho Department of Fish and Game, 3101 South Powerline Road, Nampa, Idaho 83686-8451, USA

Kevin A. Meyer*
Idaho Department of Fish and Game, 1414 East Locust Lane, Nampa, Idaho 83686-8451, USA

Martin K. Koenig
Idaho Department of Fish and Game, 600 South Walnut Street, Boise, Idaho 83712, USA

Ninh V. Vu and Matthew R. Campbell
Idaho Department of Fish and Game, 1800 Trout Road, Eagle, Idaho 83616, USA

Abstract
Anglers value alpine lakes as providing a scenic, backcountry fishing experience that is seldom found in other fisheries. However, trout introduced into alpine lakes often pose a risk to native salmonids in downstream habitats by establishing source populations in headwater locations. Although the stocking of sterile triploid trout can reduce this risk, poststocking performance should be equivalent to that of diploid fish before fisheries managers and anglers consider triploid stocking to be ideal. In this study, three different mechanical pressure treatments were tested to create mixed-sex triploid Westslope Cutthroat Trout *Oncorhynchus clarkii lewisi*; at 65,500.19 kPa (9,500 psi) applied for 5 min at 300 Celsius-minutes after fertilization, triploid induction rates were 100%, and egg survival to eye-up was only 8% lower than that for diploids. Fry were stocked into 51 alpine lakes (25 with triploids and 26 with diploids), and fish were sampled 3 years later. Gill-net catch rates, growth, and condition did not differ between stocked diploid and triploid fish. General linear models revealed that test fish were larger and in better condition in lakes with fewer total fish (indicating a density-dependent influence on growth and condition) and were also in better condition in lower-elevation lakes containing a higher percentage of shallow habitat. Ploidy level was not included in the most plausible model for any of the response variables. Our results indicate that triploid Westslope Cutthroat Trout can easily be created by using pressure treatment of fertilized eggs and appear to be a suitable alternative to diploids in alpine lake stocking programs. Our study suggests that the use of triploid Westslope Cutthroat Trout in alpine lakes similar to those we studied would prevent hybridization with native salmonids in adjacent habitats without reducing the abundance, size, or condition of fish available to anglers in the lakes where they are stocked.

Most alpine lakes in western North America lie in cirque basins formed by receding glaciers, and typically these lakes were historically fishless (Dunham et al. 2004). However, over the last century, many alpine lakes have been stocked with hatchery trout in an effort to diversify angling opportunities. Indeed, alpine lakes provide a unique fishing opportunity, with solitude, dramatic scenery, and a backcountry experience seldom found in other

*Corresponding author: kevin.meyer@idfg.idaho.gov
Received July 11, 2018; accepted November 15, 2018

fisheries. Not surprisingly, anglers visiting alpine lakes typically express high levels of satisfaction with their fishing experience (WGFD 2002; IDFG 2007). Although the stocking of fish in alpine lakes is popular among anglers who target remote settings, such stocking poses a potential risk to native amphibians in alpine lakes and streams (Knapp et al. 2001) as well as to native salmonids in downstream habitats via competition and/or hybridization (Dunham et al. 2004).

The use of triploid hatchery trout in alpine lake stocking programs is one way to prevent nonnative salmonids from establishing undesirable wild populations because triploid salmonids are functionally sterile. Triploid fishes are commonly produced by heat- or pressure-shocking the eggs soon after fertilization (reviewed by Maxime 2008 and Piferrer et al. 2009), but procedures that result in 100% triploid induction can vary even for species within the same family (e.g., Benfey and Sutterlin 1984; Piferrer et al. 1994; Cotter et al. 2000; Kozfkay et al. 2005; Preston et al. 2013) and have not yet been perfected for various salmonids, including Cutthroat Trout *Oncorhynchus clarkii* (Kozfkay et al. 2006). Treatments to induce triploidy have consistently been shown to reduce egg and sac fry survival (e.g., Happe et al. 1988; Guo et al. 1990), although performance differences between diploid and triploid fish from sac fry to stocking size are generally less consistent (Withler et al. 1998; Wagner et al. 2006; Taylor et al. 2011).

Although previous studies have shown variability in prerelease performance between diploid and triploid fish, most studies investigating fishery performance after stocking have found reduced survival for triploids. Reduced postrelease survival for triploid fish has been demonstrated for Rainbow Trout *O. mykiss* in particular (Simon et al. 1993; Brock et al. 1994; Koenig and Meyer 2011; Koenig et al. 2011) but also for Coho Salmon *O. kisutch* (Rutz and Baer 1996) and Atlantic Salmon *Salmo salar* (Cotter et al. 2000). Reduced triploid survival has been attributed to a combination of having fewer red blood cells, lower total blood hemoglobin (Benfey and Sutterlin 1984; Benfey 1999), a reduced hemoglobin–oxygen loading capacity (Graham et al. 1985), and a reduced anaerobic capacity (Hyndman et al. 2003; Scott et al. 2014). Differences in survival as a result of these physiological shortcomings become most apparent when triploid hatchery trout are stocked in challenging conditions, such as waters with low dissolved oxygen (Simon et al. 1993; Yamamoto and Iida 1994) or higher temperature (Ojolick et al. 1995). Hatchery trout are often stocked in chronically stressful waters because wild trout typically cannot support a robust fishery in such environments. Although pristine in setting, alpine lakes can be challenging environments for hatchery trout due to short growing seasons, inconsistent food sources, and low dissolved oxygen during winter months (Donald and Anderson 1982; Bailey and Hubert 2003), when most alpine lakes are covered by ice and heavy snow.

Although reduced postrelease survival for triploid hatchery trout should be expected, it is not a foregone conclusion. In fact, some studies have demonstrated equivalent poststocking survival for diploid and triploid trout stocked in lotic (Dillon et al. 2000) and lentic settings (Teuscher et al. 2003). In aquaculture settings, triploid fish have a growth advantage over diploid fish because they do not expend energy on gonadal development (Ihssen et al. 1990); however, such growth advantages have rarely been manifested in the wild (Ojolick et al. 1995; Koenig et al. 2011; Koenig and Meyer 2011; but see Teuscher et al. 2003). In addition to differences in growth and survival between diploid and triploid fish, behavioral differences have also been noted. Of particular interest is a study by Warrillow et al. (1997), who found that while both diploid male and female Brook Trout *Salvelinus fontinalis* emigrated from Adirondack lakes during spawning, only male triploids emigrated. This suggests that the stocking of triploids could result in a higher percentage of stocked fish remaining in alpine lakes once stocked, potentially maintaining higher trout densities over the long term.

None of the above-mentioned diploid–triploid postrelease comparisons has been conducted with Cutthroat Trout. The Idaho Department of Fish and Game currently stocks about 700 of the state's estimated 3,000 alpine lakes, often using diploid Westslope Cutthroat Trout *O. clarkii lewisi*. Downstream migration of diploid fish that are stocked in alpine lakes could lead to intraspecific hybridization with native Westslope Cutthroat Trout or interspecific hybridization with native Redband Trout *O. mykiss gairdneri*. Thus, fisheries managers are faced with the quandary of being reluctant to stock diploid Cutthroat Trout in headwater lakes due to hybridization concerns while also being reluctant to stock triploid fish if they provide an inferior fishery for alpine lake anglers. Considering the remaining uncertainty with regard to triploid poststocking performance, the following objectives were established for this study: (1) develop a procedure to induce 100% triploidy for Westslope Cutthroat Trout by using mechanical pressure treatment; (2) test whether the known physiological shortcomings of triploids (as noted above) result in measurable differences in survival, growth, and condition between triploid and diploid Westslope Cutthroat Trout stocked in alpine lakes; and (3) test whether certain lake characteristics or density-dependent factors influence survival, growth, and condition of Westslope Cutthroat Trout stocked in alpine lakes. We hypothesized that diploids would survive better than triploids but would have similar growth and condition and that the reduced survival of triploids could be compensated for by simply stocking more fish. Therefore, stocking density was of particular interest with regard to its influence on abundance of adult-sized stocked fish and whether this differed between ploidies.

METHODS

Triploid development.— Westslope Cutthroat Trout stocked throughout Idaho originate from the Idaho Department of Fish and Game's broodstock facility at Cabinet Gorge Fish Hatchery, which were originally domesticated from populations in the Priest River basin. An experiment to induce triploidy in Westslope Cutthroat Trout eggs was conducted at the hatchery in 2010 using hydrostatic pressure. Previous pressure treatment studies have shown that the duration and level of applied pressure are relatively consistent between species, but the time post-fertilization to most effectively inhibit the shedding of the third polar body can be variable (Kozfkay et al. 2006). Therefore, three treatments were tested using the same pressure (65,500.19 kPa [9,500 psi]) and treatment duration (5 min), but the pressure treatment was applied at three different times after fertilization: 300, 350, and 400 Celsius-minutes after fertilization (CMAF; water temperature × time). There were three replicates of each treatment and a control. Eggs from 19–23 females were pooled together for each replicate. Approximately equal numbers of eggs were split four ways (three treatments and one control) from the pooled eggs and then were fertilized using pooled milt from four to five males and activated with water. Egg survival was calculated as the number of spawned eggs that survived to the eye-up stage.

Fry were reared to approximately 50 mm TL, at which time blood samples were collected to determine triploid induction rates. Blood was collected by caudal severance, stored in Alsever's solution, and shipped to North Carolina State University, where ploidy was determined with flow cytometry. Fifty microliters of each blood sample were pipetted into 1.6 mL of a staining buffer containing 6-diamidino-2-phenylindole at 5 mg/L. Genome size relative to a known diploid control was determined using a flow cytometer (Partec PA-I), with fluorescence excitation provided by a mercury arc lamp. A minimum of 5,000 nuclei was analyzed for each sample. Up to 50 blood samples were collected per treatment replicate where possible, but some replicates with poor survival had as few as 20 fish remaining, in which case all fish were sampled. The triploid induction rate was calculated as the proportion of fish that were triploid out of the total tested in each replicate.

Egg collection and rearing.— In 2011 and 2013, triploid eggs were created at Cabinet Gorge Fish Hatchery using standard spawning techniques followed by pressure treatment to induce triploidy. Approximately 120 female Westslope Cutthroat Trout were used to collect about 100,000 triploid eggs for rearing to the fry stage, assuming roughly 50% survival to the eyed-egg stage (based on previous salmonid triploid experience). Batches of eggs from 20–30 females were pressure treated to induce triploidy using the most successful pressure treatment derived above. Diploid fish were obtained in the same fashion, with the exception of the pressure treatment process. These fish were reared separately from the triploid group. After eye-up, eggs were transferred to McCall Fish Hatchery for rearing.

Both diploid and triploid test fish were marked with adipose fin clips while rearing at McCall Fish Hatchery to differentiate them from previously stocked or naturally produced trout in our study lakes. Prior to stocking, 100 triploid and 10 diploid blood samples were collected to estimate triploid induction rates using the same methods described above. Just prior to stocking, fish from both the triploid and diploid groups were sampled to characterize mean TL (mm), weight (g), and relative weight (W_r) using the formula

$$W_r = (W/W_s) \times 100,$$

where W = actual fish weight; and W_s = a standard weight for fish of the same length (Anderson and Neumann 1996).

Selecting study lakes.— In total, 51 lakes were selected for one-time stocking of test fish (26 stocked with diploids and 25 stocked with triploids) by use of fixed-wing aircraft as part of the routine 2011 and 2013 (August and September) stocking requests for the specified lakes (see Supplemental Table S1 for lake-specific data available in the online version of this article). Diploid and triploid marked fish were stocked into separate lakes to avoid any potential competition between the ploidy test groups that might influence postrelease performance (Kozfkay et al. 2006; Koenig et al. 2011). All study lakes were on 3-year stocking rotations and thus had last been stocked 3 years prior to receiving test fish. Study lakes were chosen throughout central Idaho to encompass a wide geographical range, but sampling efficiency (i.e., distance from trailhead and some targeted clustering of lakes to maximize data collection for each field trip) was also considered when selecting study lakes. Diploid or triploid stocking for each lake chosen for inclusion in our study was assigned randomly.

All lakes were open to harvest with a six-fish bag limit, but angler harvest of trout in Idaho alpine lakes is negligible. This is evidenced by the fact that as part of this and a companion study, we released a total of 943 anchor-tagged fish (wild and stocked fish combined) in 22 alpine lakes and had five tags reported by anglers. Considering that Idaho anglers report about 50% of the anchor tags they encounter in landed trout (Meyer et al. 2012), this translates to an estimated harvest of about 1%. Moreover, distance from the nearest trailhead was equivalent between diploid alpine lakes (mean = 3.1 km; range = 0–11 km) and triploid lakes (mean = 3.6 km; range = 0–12 km), making test fish of either ploidy equally vulnerable to angler effort and harvest. Overall, 18,450 diploids and 17,700 triploids were stocked. The number of test fish stocked in each lake was determined by the standard annual request for that location, resulting in a wide range of stocking densities (13–578 fish/ha).

Poststocking evaluation.— All lakes were sampled 3 years after stocking so that stocked fish could grow to a size desirable to anglers. Two, three, or four floating experimental gill nets were set per lake depending on lake size, shape, and depth. However, in general, we set two nets at lakes smaller than 1 ha; three nets at lakes between 1 and 4 ha; and four nets at lakes greater than 4 ha (correlation coefficient between number of gill nets and lake size: $r = 0.74$). Gill nets (46 m long and 1.5 m deep) consisted of nylon-mesh panels with 19-, 25-, 30-, 33-, 38-, and 48-mm bar mesh; they were set perpendicular to the shoreline in mid- to late afternoon and were retrieved the next morning. Captured fish were identified to species, checked for an adipose fin clip, measured to the nearest millimeter (TL), and weighed to the nearest gram. In 2016, a tissue sample was taken from all adipose-clipped trout to genetically assign sex to the test fish and determine whether there were any differences in sex ratio between diploid and triploid groups.

We measured several lake characteristics (Table 1) that have been previously shown to be related to trout size (length or weight) and abundance in alpine lakes (e.g., Donald et al. 1980; Chamberlain and Hubert 1996; Rabe 2001; Bailey and Hubert 2003). Elevation (m) and surface area (ha) were determined using Google Earth Pro (Google 2013). The shoreline development ratio (calculated as $L/\left[2\sqrt{\pi A}\right]$, where L = length of the shoreline; A = lake surface area) is a measure of the shoreline length of a given lake relative to the shoreline length of a perfectly circular lake of equal area, with perfectly circular lakes having a value of 1.0; this measurement was also taken from Google Earth Pro. Aspect affects solar input and therefore primary productivity in lakes, and primary productivity is often directly related to fish production (Downing et al. 1990); as such, we categorized aspect as good (south-, southeast-, and southwest-facing lakes), fair (east- and west-facing lakes), or poor (north-, northeast-, and northwest-facing lakes). Stocking density was calculated as the number of fish stocked divided by the estimated surface area (fish/ha). Lake distance (km) from the nearest maintained trail was also measured from maps and was used as an index of angler accessibility, which we considered a surrogate for fishing pressure (cf. Bailey and Hubert 2003). At the time of the fish surveys, the percentage of shallow water (i.e., <2 m deep) in the lake was visually estimated because shallower lakes are generally more productive. The ranges in values for all of these characteristics were very similar for diploid- and triploid-stocked lakes (Table 1; also see Table S1); for continuous variables, we formally tested for differences using two-sample t-tests but found no differences ($P \geq 0.44$ for all comparisons).

Genetic analyses.— Restriction site-associated DNA sequencing was used to identify sex-specific markers to estimate the proportion of captured test fish in 2016 (both diploid and triploid) that were males or females. This method uses a restriction enzyme to cut the genome of reference males and females and then sequence 100–300 base pairs that flank the restriction site and the resulting DNA fragments. This technology is a particularly powerful tool for exploring genetic variation in "nonmodel" species because it does not require a fully sequenced genome

TABLE 1. Means and ranges of lake and fish characteristics measured at 51 alpine lakes in Idaho where either diploid or mixed-sex triploid Westslope Cutthroat Trout were stocked as fry and sampled 3 years later (W_r = relative weight). See Table S1 for lake-specific data.

	Diploid-stocked lakes		Triploid-stocked lakes	
Lake characteristic	Mean	Range	Mean	Range
Elevation (m)	2,226	1,639–2,472	2,199	1,345–2,525
Surface area (ha)	3.1	0.5–11.8	3.7	0.3–11.8
Proportion shallow habitat	0.21	0.02–0.80	0.22	0.03–1.00
Stocking density (fish/ha)	96	15–500	91	14–578
Shoreline development ratio	1.25	1.10–2.00	1.33	1.06–2.31
Distance from nearest trail (km)	3.1	0.0–11.0	3.6	0.0–12.0
CPUE of test fish (number/net-hour)	0.18	0.00–0.52	0.15	0.00–0.49
TL of test fish (mm)	294	217–372	291	220–353
W_r of test fish	97.5	82.1–108.3	95.5	75.4–128.6
CPUE of nontest fish (number/net-hour)	0.54	0.00–3.02	0.40	0.00–2.59

(Gamble and Zarkower 2014). We screened 10 phenotypic males and 10 phenotypic females using the *Pst*-I restriction enzyme. We identified two single-nucleotide polymorphic (SNP) markers (*WCT_245656_41* and *WCT_138669_65*) that yielded patterns of high genotyping success and differentiated genetic sex in test samples. These SNP markers were converted into TaqMan assays (primer/probe sequences and PCR conditions are available from the authors upon request). The accuracy of these markers was further tested with a screening of 90 phenotypic females and 90 phenotypic males from the Kings Lake broodstock of Westslope Cutthroat Trout. Of the 180 samples, 175 (97.2%) exhibited concordance between phenotypic sex and genetic sex. All five of the discrepancies were from phenotypic males that genotyped as genetic females. Because 100% concordance was observed among genotyping calls between the two markers, only *WCT_138669_65* was screened on study samples.

Data analyses.— Prior to stocking, the mean TL and mean W_r of test fish were compared using two-sample *t*-tests. For poststocking evaluations, each lake was considered the unit of observation for all analyses. For each lake, CPUE was calculated as the number of test fish captured per net-hour fished; CPUE was considered an index of the abundance of test fish in the lake. There was a strong correlation between catch per net-hour and catch per net-night ($r = 0.93$); thus, data analyses were essentially identical regardless of which catch metric was used. Mean TL and mean W_r of test fish were also estimated for each lake as indices of fish growth and fish condition. Two-sample *t*-tests were used to assess whether CPUE, mean TL, and mean W_r of test fish differed between diploid and triploid groups.

To evaluate whether lake characteristics affected CPUE, growth, or condition of test fish, all independent variables (i.e., lake characteristics) were first plotted individually against all three response variables (CPUE, mean TL, and mean W_r) to look for data outliers, nonlinear relationships, and heteroscedasticity. Because naturally produced or previously stocked trout were encountered in 45 of the 51 study lakes, the abundance (i.e., CPUE) of nontest fish was included as a predictive variable to account for potential density-dependent effects on the survival (i.e., abundance) of stocked test fish. For mean TL and mean W_r analyses, density dependence was evaluated by relating these two metrics to the CPUE of all fish sampled. Scatterplots indicated that these two relationships were nonlinear; thus, they were $\log_e$ transformed prior to the remaining analyses.

General linear models were then developed for each response variable separately. Candidate models for each response variable were limited to all potential single-factor models as well as the best multiple-factor model if that model was superior to any of the single-factor models. Candidate models were ranked using Akaike's information criterion corrected for small sample size (AIC_c; Burnham and Anderson 2002), and the amount of variation explained by each model was compared using r^2 values. Ploidy was also included as an explanatory variable, and year was included because of the between-year difference in fish condition at the time of stocking.

Because sample sizes were too small to reliably estimate the sex ratio of test fish at each lake, data were pooled across lakes to evaluate whether the sex ratio of test fish was skewed toward females in triploid lakes compared to diploid lakes, as would result if diploid males and females both engaged in spawning migrations that resulted in some emigration from lakes, but only male triploids engaged in such migrations (Warrillow et al. 1997). Sex ratios were compared between ploidy groups by calculating a 95% confidence interval (CI) around the difference between the two proportions (Johnson 1999; Fleiss et al. 2003); the difference was considered statistically significant if the calculated CI did not include zero. All statistical analyses were conducted using SAS software (SAS Institute 2009) with $\alpha = 0.05$.

RESULTS

Triploid Development

Triploid induction rates were very similar across all three treatments (Table 2). The 300- and 350-CMAF treatments both showed 100% triploid induction rates across all three replicates, whereas the 400-CMAF treatment had two replicates of 100% triploid induction and one replicate of 98% triploid induction. Survival to eye-up was highest for the control group (31% on average), followed by the 300-CMAF test group (27% on average). Mean survival to eye-up was much lower for the 350-CMAF (16%) and 400-CMAF (18%) test groups. Eye-up survival rates were low for all egg lots from replicate 1, including controls, suggesting poor egg quality for that group. When eggs from replicate 1 were excluded, mean eye-up survival rates ranged from 21% to 38% across all treatments and the control. The 300-CMAF treatment (65,500.19 kPa [9,500 psi]; 5 min) returned the best combination of induction rate and survival to eye-up; therefore, this treatment was used to develop triploid eggs for the rest of our study.

Egg Collection and Rearing

For the 2011 egg take, eye-up survival rates between the two test groups were similar to those observed during triploid development trials, with the eye-up rate for triploids (41%) being slightly lower than that for diploids (48%). For eggs collected in 2013, eye-up survival rates were higher and virtually identical for diploids (57%) and

TABLE 2. Percent eye-up and percent triploidy (mean and range) for controls and three pressure treatment groups of fertilized Westslope Cutthroat Trout eggs treated at 65,500.19 kPa (9,500 psi) for 5 min at varying Celsius-minutes after fertilization (CMAF). Sample size (n) indicates the number of replicates of each treatment.

		Percent eye-up		Percent triploid	
Treatment	n	Mean	Range	Mean	Range
Control	3	31	13–45		
300 CMAF	3	27	7–38	100.0	100–100
350 CMAF	3	16	8–27	100.0	100–100
400 CMAF	3	18	6–25	99.3	98–100

triploids (56%). Triploid induction rates were 100% in both 2011 and 2013.

At the time of stocking, the average TL and W_r of diploid fish in 2011 (42.8 mm and 121.5, respectively) were very similar to those of triploid fish (44.2 mm and 112.9); neither the TL (t = 1.33, P = 0.18) nor the W_r (t = 1.21, P = 0.23) of test fish differed statistically between ploidy groups. In 2013, the average TL of diploid fish (42.0 mm) and triploid fish (41.1 mm) again did not differ statistically (t = 1.77, P = 0.08); however, the mean W_r values of diploid fish (130.4) and triploid fish (80.8) were significantly different (t = 35.93, P < 0.001; Figure 1).

Poststocking Evaluation

In total, 1,322 fish were caught in gill nets across all 51 test lakes; 345 of the captured individuals were test fish. The remaining captured fish included wild or previously stocked Westslope Cutthroat Trout (743 fish; present in 42 lakes); wild Rainbow Trout and/or Rainbow Trout × Cutthroat Trout hybrids (56 fish; present in six lakes); wild Brook Trout (154 fish; present in six lakes); and stocked Arctic Grayling *Thymallus arcticus* from a 2010 planting event (24 fish; stocked in one lake). Although a few (n < 20) of the nonadipose-clipped Cutthroat Trout were large enough to have been from the stocking event prior to ours (i.e., 6-year-old stocked fish), the vast majority were either smaller than the smallest test fish (30%) or overlapped test fish in size (68%), indicating that they were likely the same age or younger than test fish and were thus wild Cutthroat Trout. Of the 26 lakes stocked with diploid trout, 22 contained test fish; 19 of the 25 lakes stocked with triploids contained test fish. Wild trout were present in 44 of the 51 test lakes, including 36 lakes where they were sympatric with test fish.

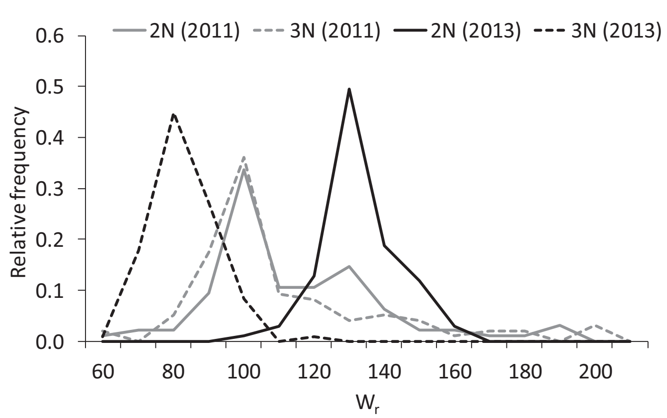

FIGURE 1. Relative weights (W_r) of diploid (2N) and mixed-sex triploid (3N) Westslope Cutthroat Trout fry prior to stocking into Idaho alpine lakes during 2011 and 2013.

Mean gill-net CPUE across both study years was 0.18 fish/net-hour for diploid test fish compared to 0.15 fish/net-hour for triploid test fish and did not differ statistically between the two ploidy groups (t = 0.69, P = 0.49). Average TL of test fish at each lake was 294 mm for diploids and 291 mm for triploids and did not differ significantly between the two groups (t = 0.26, P = 0.79). Mean W_r of test fish was 97.5 in lakes stocked with diploid test fish and 95.5 in lakes stocked with triploid test fish; mean W_r was not statistically different between the groups (t = 0.54, P = 0.59).

The general linear models developed to analyze factors potentially influencing CPUE, mean TL, and W_r in alpine lakes showed that most of the factors we measured had little to no effect on the poststocking performance of test fish (Table 3). For the CPUE models, the best model indicated that the catch of test fish was higher at lakes with more shoreline relative to the size of the lake (Table 4). There was nearly three times more support for this model than for the next-best model, which indicated that the catch of test fish was higher at smaller lakes. However, even the best model explained only 6% of the variation in CPUE of test fish between lakes.

For the fish TL models, the best model indicated that test fish were larger in lakes with fewer total fish, and this model explained 28% of the variation in mean fish TL across all lakes (Tables 3, 4). There was very little support for any other models of fish TL. For W_r, the best model indicated that test fish condition was higher in lower-elevation lakes containing a higher percentage of shallow habitat, with fewer total fish, and that were stocked in 2011 rather than 2013 (Tables 3, 4). The best model explained 41% of the variation in mean W_r of test fish, and there was very little support for any other W_r models.

Thus, the effect of density dependence on test fish was evident in fish growth and condition models but not the abundance model. This was also evident when examining scatterplots of all three dependent variables (CPUE, fish TL, and W_r) plotted against density-dependent terms (Figure 2), which depicted a statistically significant and exponential decline in mean TL (r^2 = 0.28; F = 15.00, P < 0.001) and W_r (r^2 = 0.24; F = 11.49, P = 0.002) of

TABLE 3. Model results relating the CPUE, TL, and relative weight (W_r) of test fish to various lake and fish characteristics at 51 alpine lakes in Idaho where either diploid or mixed-sex triploid Westslope Cutthroat Trout were stocked as fry and sampled 3 years later (AIC_c = Akaike's information criterion corrected for small sample size; ΔAIC_c = AIC_c difference; w_i = Akaike weight).

Model	AIC_c	ΔAIC_c	w_i	r^2
CPUE models				
Shoreline development (best model)	−136.42	0.00	0.33	0.06
Surface area	−134.53	1.89	0.13	0.03
Stocking density	−133.91	2.51	0.09	0.02
CPUE of nontest fish	−133.72	2.71	0.08	0.01
Percent shallow habitat	−133.71	2.71	0.08	0.01
Ploidy	−133.52	2.90	0.08	0.01
Elevation	−133.02	3.40	0.06	0.00
Distance from nearest trail	−133.02	3.40	0.06	0.00
Year	−133.01	3.41	0.06	0.00
Aspect	−131.46	4.96	0.03	0.02
Fish TL models				
Log_e(CPUE of all fish) (best model)	338.04	0.00	0.96	0.28
Elevation	346.89	8.85	0.01	0.10
Stocking density	347.11	9.07	0.01	0.10
Shoreline development	349.38	11.34	<0.01	0.05
Aspect	350.21	12.17	<0.01	0.08
Year	350.27	12.23	<0.01	0.03
Percent shallow habitat	350.38	12.34	<0.01	0.02
Surface area	350.62	12.59	<0.01	0.02
Distance from nearest trail	351.20	13.16	<0.01	0.00
Ploidy	351.30	13.27	<0.01	0.00
W_r models				
Log_e(CPUE of all fish) + year + percent shallow habitat + elevation (best model)	211.14	0.00	0.93	0.41
Log_e(CPUE of all fish)	216.59	5.45	0.06	0.24
Elevation	222.43	11.30	<0.01	0.13
Year	223.42	12.29	<0.01	0.11
Stocking density	226.21	15.07	<0.01	0.11
Distance from nearest trail	226.60	15.46	<0.01	0.03
Ploidy	227.43	16.29	<0.01	0.01
Surface area	227.51	16.37	<0.01	0.01
Shoreline development	227.82	16.68	<0.01	0.01
Aspect	228.33	17.19	<0.01	0.05
Percent shallow habitat	228.72	17.59	<0.01	0.01

test fish as the total abundance of fish in the lakes increased but no decline in the catch of test fish as the abundance of nontest fish increased (r^2 = 0.02; F = 0.78, P = 0.38). Ploidy was not included in the most plausible model (based on AIC_c weights) for any of the response variables. Likewise, stocking density was not related to the CPUE of test fish and did not differ between ploidies (Figure 3).

Results from fish sampled in 2016 showed that the sex ratios of adult test fish remaining in the lakes was variable (Figure 4). Overall, the proportion (±95% CI) of the catch that was female in triploid-stocked lakes (0.55 ± 0.12) was slightly higher than that in diploid-stocked lakes (0.48 ± 0.12) but did not differ statistically (difference between groups = 0.07; 95% CI = −0.12 to 0.25). Thus, there was no evidence that a higher proportion of diploid females was emigrating from lakes relative to triploid females.

DISCUSSION

The overarching goal of our research was to develop a reliable procedure for inducing 100% triploidy in hatchery Westslope Cutthroat Trout fry to be stocked into alpine

TABLE 4. Coefficients and 95% confidence intervals (CIs) for the most highly supported models relating CPUE, mean TL, and mean relative weight (W_r) of test fish to various lake and fish characteristics at 51 alpine lakes in Idaho where either diploid or mixed-sex triploid Westslope Cutthroat Trout were stocked as fry and sampled 3 years later.

Coefficient	Estimate	±95% CI
CPUE model		
Intercept	−0.033	0.210
Shoreline development	0.151	0.160
Fish TL model		
Intercept	273.224	14.532
Log_e(CPUE of all fish)	−25.322	12.815
W_r model		
Intercept	108.782	29.278
Log_e(CPUE of all fish)	−5.869	3.639
Year (2011)	9.456	5.922
Percent shallow habitat	16.789	13.734
Elevation	−0.012	0.013

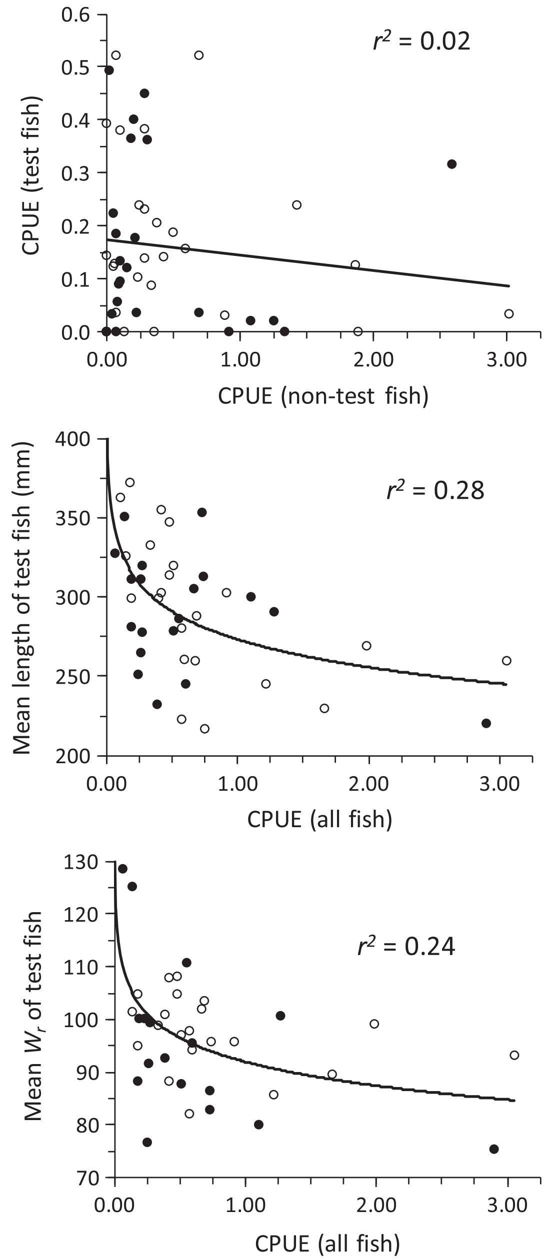

FIGURE 2. Scatterplots of potential density-dependent relationships for CPUE, mean TL, and relative weight (W_r) of diploid (open circles) and mixed-sex triploid (filled circles) Westslope Cutthroat Trout (test fish) that were stocked as fry into 51 alpine lakes in Idaho and sampled 3 years later. Coefficients of determination (r^2) and least-squares linear regression lines are also depicted. Logarithmic trends were fitted to test fish mean TL and W_r, whereas a linear trend was fitted to test fish CPUE due to a poor logarithmic fit.

lakes and to evaluate whether those fry survived and grew to a similar size as diploid fish stocked in similar alpine lakes. Hydrostatic pressure treatment proved to be an effective way to create triploid hatchery Westslope Cutthroat Trout, and our procedure was similar to those previously found to be effective for various salmonids (Teskeredžić et al. 1993; Kozfkay et al. 2005, 2006). As expected, the eye-up survival rate for triploid eggs was slightly lower than that for diploids, but this can usually be mitigated during the egg take process by spawning more fish.

Prior to stocking, fish condition was lower for triploid fingerlings in one year, but this did not result in reduced poststocking fish condition 3 years later. Previous work comparing prestocking hatchery growth of diploid and triploid trout has been highly variable, with some studies demonstrating that triploid hatchery trout grew better than diploids prior to stocking (Simon et al. 1993; Sheehan et al. 1999) and other studies demonstrating the opposite effect (Myers and Hershberger 1991) or no difference (Wagner et al. 2006). Considering this variability in prestocking performance among studies and the potential low eye-up rates for triploid eggs, hatchery staff should closely monitor growth and survival of triploid trout in-hatchery to meet the stocking goals typically set for diploids.

Three years after being stocked into alpine lakes, mixed-sex triploid Westslope Cutthroat Trout had survival, growth, and condition that were equivalent to those of diploids. These results concur with a previous study demonstrating equivalent performance of mixed-sex triploid and diploid Brook Trout stocked in alpine lakes (Budy et al. 2012) but contrast with a study in which diploid Rainbow Trout survival was higher than survival for mixed-sex triploids stocked in alpine lakes (Koenig et al. 2011). Authors of the latter study suggested that because diploid and triploid fish were stocked into the same waters, competition rather than inherently lower performance may have explained the differential survival they observed, but Budy et al. (2012) directly evaluated some aspects of competition

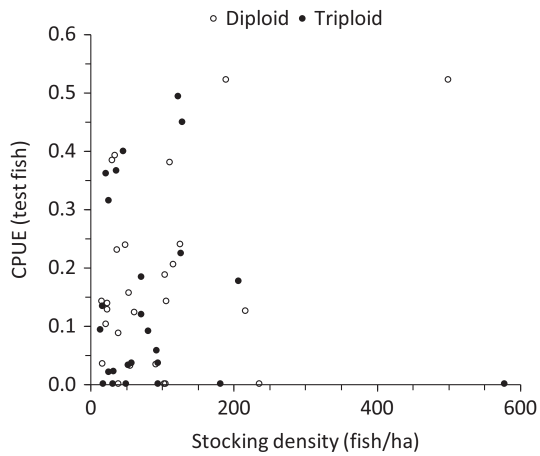

FIGURE 3. Scatterplot of stocking density for diploid (open circles) and mixed-sex triploid (filled circles) Westslope Cutthroat Trout (test fish) that were stocked as fry into 51 alpine lakes in Idaho and the subsequent CPUE of test fish during sampling conducted 3 years later.

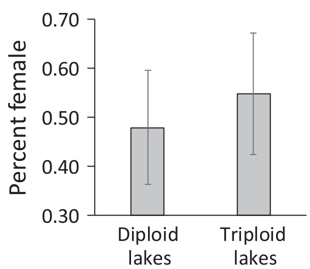

FIGURE 4. Sex composition (percent female) of diploid and triploid Westslope Cutthroat Trout 3 years after the fish were stocked into 51 alpine lakes in Idaho (2013 stocking event). Error bars depict 95% confidence intervals.

and observed no differences between diploids and triploids in terms of diet or aggressive behavior. In the present study, by stocking groups independently, year-class-specific competition was removed as a potential confounding factor. With fry survival and growth in alpine lakes being apparently equivalent between diploid and triploid Westslope Cutthroat Trout, at least in the lakes we studied, the clear advantage of using triploids in alpine lake stocking programs is that the concern over hybridization of stocked fish with native salmonids is virtually eliminated.

Out-migration of trout stocked in alpine lakes has been documented by other authors (Warrillow et al. 1997; Adams et al. 2001; Daniels et al. 2008) and can create two potential problems, both of which can be circumvented by the stocking of triploid fish. First, stocking of triploids reduces the potential risk of out-migrating fish colonizing adjacent waters and threatening the persistence of native salmonids via competition or introgressive hybridization. Second, although sterile males display external sexual characteristics and migrate to spawning areas at rates similar to those of diploid males, sterile females may not (Warrillow et al. 1997). Hence, the use of all-female triploid trout in alpine lake stocking programs could potentially halt spawning-related out-migration altogether. In fact, all-female triploid Rainbow Trout stocked in alpine lakes outperformed diploid and mixed-sex triploid fish by a 3:1 and 11:1 ratio, respectively (Koenig et al. 2011), although the role out-migration played in these differences was not investigated. While not statistically different in the present study, the slightly higher percentage of females (determined genetically) in triploid-stocked waters relative to diploid-stocked waters was intriguing, but this slight skewness was not statistically significant and was in the same direction as the genotype–phenotype discordance mentioned above. Having sampled at 3 years after stocking, we may have collected fish too early to detect a significant shift in sex ratio stemming from spawning migrations, though the size and age of our test fish should have resulted in many fish being mature. Further research on gender-specific out-migration rates and the feasibility of creating all-female fry for stocking is needed to determine whether the excess costs and labor of creating all-female triploids are justified by a higher percentage of stocked trout remaining in receiving waters for anglers to catch.

With a robust sample size of lakes and a wide range of stocking densities in our study, we anticipated some sort of density-dependent relationship between stocking density and CPUE of stocked fish (cf. Bailey and Hubert 2003) that might provide fisheries managers with better guidelines on how many fish to stock in a given alpine lake and that might indicate whether stocking rates should be different for diploids and triploids. However, stocking density explained almost none of the variability in CPUE of stocked Westslope Cutthroat Trout and little of the variability in their growth and condition. Any relationship between stocking density and stocked fish abundance in the present study may have been masked by the fact that 74% of the fish caught were nontest fish. Thus, in most cases, the number of fish stocked had little influence on total fish abundance in the lake, as evidenced by the weak correlation between stocking density and CPUE of all fish (r = 0.05). There was a strong density-dependent response of test fish growth and condition to the total number of fish caught; such density-dependent signals are common in trout fisheries within alpine lakes (Hall 1991; Walters and Post 1993; Parker et al. 2007; Messner 2017).

Although we measured only some of the lake characteristics that have been previously shown to influence salmonid growth and survival in alpine lakes, the only metrics that had any appreciable relationship to poststocking performance of Westslope Cutthroat Trout were elevation, the percentage of the lake that was shallow, and the amount of shoreline relative to the size of the lake.

Lower-elevation lakes grew larger fish that had better condition, as has been demonstrated previously for alpine lakes (Donald et al. 1980). Although elevation likely did not have a causative effect on fish growth or condition, elevation in alpine lakes is often correlated with other physiochemical conditions that we did not measure, such as water temperature and conductivity, both of which have been shown to affect fish growth in alpine lakes (Donald et al. 1980; Chamberlain and Hubert 1996; Bailey and Hubert 2003). Shallow habitat has long been associated with increased lake productivity for fish (Moyle 1949; Northcote and Larkin 1956), including alpine lakes (Chamberlain and Hubert 1996).

The results of the present study are encouraging for triploid Westslope Cutthroat Trout poststocking performance in alpine lakes, but future research to corroborate or refute our findings could be valuable for several reasons. First, there was tremendous environmental variation among study lakes, only part of which was captured in the limited lake characteristics that we measured; other factors not accounted for in our study (e.g., zooplankton abundance, conductivity) may have contributed to the variation in postrelease performance of stocked diploids and triploids, potentially masking subtle differences in survival or growth of the stocked test groups. Second, wild trout dominated fish abundance in our study lakes; thus, our study may not have accurately described the survival and growth that would be expected of triploid and diploid Westslope Cutthroat Trout when stocked in alpine lakes lacking wild fish. Nevertheless, our results suggest that in alpine lakes like those in our study, mixed-sex triploid Westslope Cutthroat Trout are a viable alternative to diploids for fisheries managers to utilize as a put-and-grow stocking tool in lakes where the conservation of adjacent native salmonid populations is a concern. Egg takes associated with triploid groups should be adjusted to compensate for slightly lower survival to eye-up. Further research is also warranted to compare postrelease performance between mixed-sex and all-female Westslope Cutthroat Trout to evaluate whether the added cost of developing an all-female strain would be outweighed by the added survival other studies have demonstrated for all-female strains (e.g., Koenig et al. 2011).

ACKNOWLEDGMENTS

We acknowledge the staffs at Cabinet Gorge Fish Hatchery and McCall Fish Hatchery for their work in spawning, rearing, marking, and stocking the fish used in this study. Luciano Chiaramonte, Micah Davidson, Dennis Daw, Leah Gunnink, Pat Kennedy, Tony Lamansky, Liz Mamer, Kevin Nelson, Kylie Porter, Rick Raymondi, Dan Schill, Noah Starr, Luke Teraberry, Joe Thiessen, and Jennifer Vincent all assisted with lake sampling. Robert Hand, Dale Allen, and their field crews also helped with additional lake sampling. We thank Dan Schill and three anonymous reviewers for critically reviewing earlier versions of the manuscript. Funding for this work was provided by anglers and boaters through their purchase of Idaho fishing licenses, tags, and permits and from federal excise taxes on fishing equipment and boat fuel through the Sport Fish Restoration Program. There is no conflict of interest declared in this article.

REFERENCES

Adams, S. B., C. A. Frissell, and B. E. Rieman. 2001. Geography of invasions in mountain streams: consequences of headwater lake fish introductions. Ecosystems 4:296–307.

Anderson, R. O., and R. M. Neumann. 1996. Length, weight, and associated structural indices. Pages 447–482 *in* B. R. Murphy and D. W. Willis, editors. Fisheries techniques, 2nd edition. American Fisheries Society, Bethesda, Maryland.

Bailey, P. E., and W. A. Hubert. 2003. Factors associated with stocked Cutthroat Trout populations in high-mountain lakes. North American Journal of Fisheries Management 23:611–618.

Benfey, T. J. 1999. The physiology and behavior of triploid fishes. Reviews in Fisheries Science 7:39–67.

Benfey, T. J., and A. M. Sutterlin. 1984. Growth and gonadal development in triploid landlocked Atlantic Salmon (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences 41:1387–1392.

Brock, I. V., P. A. Hansen, D. N. McBride, and A. C. Havens. 1994. Culture and performance of triploid Rainbow Trout in Alaska. Transactions of the North American Wildlife and Natural Resources Conference 59:263–273.

Budy, P., G. P. Thiede, A. Dean, D. Olsen, and G. Rowley. 2012. A comparative and experimental evaluation of performance of stocked diploid and triploid Brook Trout. North American Journal of Fisheries Management 32:1211–1224.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer Verlag, New York.

Chamberlain, C. B., and W. A. Hubert. 1996. Factors affecting Brook Trout populations in lakes and reservoirs in Wyoming. Journal of Freshwater Ecology 11:301–309.

Cotter, D., V. O'Donovan, N. O'Maoiléidigh, G. Rogan, N. Roche, and N. P. Wilkins. 2000. An evaluation of the use of triploid Atlantic Salmon (*Salmo salar* L.) in minimizing the impact of escaped farmed salmon on wild populations. Aquaculture 186:61–75.

Daniels, R. A., R. S. Morse, J. W. Sutherland, R. T. Bombard, and C. W. Boylen. 2008. Fish movement among lakes: are lakes isolated? Northeastern Naturalist 15:577–588.

Dillon, J. C., D. J. Schill, and D. M. Teuscher. 2000. Relative return to creel of triploid and diploid Rainbow Trout stocked in eighteen Idaho streams. North American Journal of Fisheries Management 20:1–9.

Donald, D. B., and R. S. Anderson. 1982. Importance of environment and stocking density for growth of Rainbow Trout in mountain lakes. Transactions of the American Fisheries Society 111:675–680.

Donald, D. B., R. S. Anderson, and D. W. Mayhood. 1980. Correlations between Brook Trout growth and environmental variables for mountain lakes in Alberta. Transactions of the American Fisheries Society 109:603–610.

Downing, J. A., C. Plante, and S. Lalonde. 1990. Fish production correlated with primary productivity, not the morphoedaphic index. Canadian Journal of Fisheries and Aquatic Sciences 47:1929–1936.

Dunham, J. B., D. S. Pilliod, and M. K. Young. 2004. Assessing the consequences of nonnative trout in headwater ecosystems in western North America. Fisheries 29(6):18–26.

Fleiss, J. L., B. Levin, and M. C. Paik. 2003. Statistical methods for rates and proportions, 3rd edition. Wiley, Hoboken, New Jersey.

Gamble, T., and D. Zarkower. 2014. Identification of sex-specific molecular markers using restriction site associated DNA sequencing. Molecular Ecology Resources 14:902–913.

Google. 2013. Google Earth Pro release 7.1.2.2041. Google, Mountain View, California.

Graham, M. S., G. L. Fletcher, and T. J. Benfey. 1985. Effect of triploidy on blood oxygen content of Atlantic Salmon. Aquaculture 50:133–139.

Guo, X., W. K. Hershberger, and J. M. Myers. 1990. Growth and survival of intrastrain and interstrain Rainbow Trout (*Oncorhynchus mykiss*) triploids. Journal of the World Aquaculture Society 21:250–256.

Hall, D. L. 1991. Growth, fecundity, and recruitment responses of stunted Brook Trout populations to density reduction. Doctoral dissertation. University of British Columbia, Vancouver.

Happe, A., E. Quillet, and B. Chevassus. 1988. Early life history of triploid Rainbow Trout (*Salmo gairdneri* Richardson). Aquaculture 71:107–118.

Hyndman, C. A., J. D. Kieffer, and T. J. Benfey. 2003. The physiological response of diploid and triploid Brook Trout to exhaustive exercise. Comparative Biochemistry and Physiology A 134:167–179.

IDFG (Idaho Department of Fish and Game). 2007. Fisheries management plan, 2007–2012. IDFG, Boise.

Ihssen, P. E., L. R. McKay, I. McMillan, and R. B. Phillips. 1990. Ploidy manipulation and gynogenesis in fishes: cytogenetic and fisheries applications. Transactions of the American Fisheries Society 119:698–717.

Johnson, D. 1999. The insignificance of significance testing. Journal of Wildlife Management 63:763–772.

Knapp, R. A., K. R. Matthews, and O. Sarnelle. 2001. Resistance and resilience of alpine lake fauna to fish introductions. Ecological Monographs 71:401–421.

Koenig, M. K., J. R. Kozfkay, K. A. Meyer, and D. J. Schill. 2011. Performance of diploid and triploid Rainbow Trout stocked in Idaho alpine lakes. North American Journal of Fisheries Management 31:124–133.

Koenig, M. K., and K. A. Meyer. 2011. Relative performance of diploid and triploid catchable Rainbow Trout stocked in Idaho lakes and reservoirs. North American Journal of Fisheries Management 31:605–613.

Kozfkay, J. R., J. C. Dillon, and D. J. Schill. 2006. Routine use of sterile fish in salmonid sport fisheries: are we there yet? Fisheries 31:392–401.

Kozfkay, J. R., E. J. Wagner, and D. Aplanalp. 2005. Production of triploid Lake Trout by means of pressure treatment. North American Journal of Aquaculture 67:93–97.

Maxime, V. 2008. The physiology of triploid fish: current knowledge and comparisons with diploid fish. Fish and Fisheries 9:67–78.

Messner, J. 2017. Improving a high mountain lake fishery by stocking tiger muskellunge to control an overabundant wild Brook Trout population. Pages 243–249 *in* R. F. Carline, editor. Proceedings of Wild Trout XII Symposium: science, politics, and wild trout management —who's driving and where are we going? Wild Trout Symposium, Bozeman, Montana.

Meyer, K. A., F. S. Elle, J. A. Lamansky Jr., E. R. J. M. Mamer, and A. E. Butts. 2012. A reward–recovery study to estimate tagged-fish reporting rates by Idaho anglers. North American Journal of Fisheries Management 32:696–703.

Moyle, J. B. 1949. Some indices of lake productivity. Transactions of the American Fisheries Society 76:322–334.

Myers, J. M., and W. K. Hershberger. 1991. Early growth and survival of heat-shocked and tetraploid-derived triploid Rainbow Trout (*Oncorhynchus mykiss*). Aquaculture 96:97–107.

Northcote, T. G., and P. A. Larkin. 1956. Indices of productivity in British Columbia lakes. Journal of the Fisheries Research Board of Canada 13:515–540.

Ojolick, E. J., R. Cusack, T. J. Benfey, and S. R. Kerr. 1995. Survival and growth of all-female diploid and triploid Rainbow Trout (*Oncorhynchus mykiss*) reared at chronic high temperature. Aquaculture 131:177–187.

Parker, B. R., D. W. Schindler, F. M. Wilhelm, and D. B. Donald. 2007. Bull Trout population responses to reductions in angler effort and retention limits. North American Journal of Fisheries Management 27:848–859.

Piferrer, F., A. Beaumont, J. Falguière, M. Flajšhans, P. Haffray, and L. Colombo. 2009. Polyploid fish and shellfish: production, biology and applications to aquaculture for performance improvement and genetic containment. Aquaculture 293:125–156.

Piferrer, F., T. J. Benfey, and E. M. Donaldson. 1994. Production of female triploid Coho Salmon (*Oncorhynchus kisutch*) by pressure shock and direct estrogen treatment. Aquatic Living Resources 7:127–131.

Preston, A. C., J. F. Taylor, B. Craig, P. Bozzolla, D. J. Penman, and H. Migaud. 2013. Optimisation of triploidy induction in Brown Trout (*Salmo trutta* L.). Aquaculture 414:160–166.

Rabe, F. W. 2001. High mountain lake research natural areas in Idaho. U.S. Forest Service General Technical Report RMRS-GTR-77.

Rutz, D. S., and C. C. Baer. 1996. Comparative performance of stocked mixed-sex and all-female Rainbow Trout and triploid Coho Salmon in landlocked lakes in southcentral Alaska, 1994 and 1995. Alaska Department of Fish and Game, Fishery Data Series Number 96-23, Anchorage.

SAS Institute. 2009. SAS/STAT 9.2 user's guide, 2nd edition. SAS Institute, Cary, North Carolina.

Scott, M. A., R. S. Dhillon, P. M. Schulte, and J. G. Richards. 2014. Physiology and performance of wild and domestic strains of diploid and triploid Rainbow Trout (*Oncorhynchus mykiss*) in response to environmental challenges. Canadian Journal of Fisheries and Aquatic Sciences 72:125–134.

Sheehan, R. J., S. P. Shasteen, and A. V. Suresh. 1999. Better growth in all-female diploid and triploid Rainbow Trout. Transactions of the American Fisheries Society 128:491–498.

Simon, D. C., C. G. Scalet, and J. C. Dillon. 1993. Field performance of triploid and diploid Rainbow Trout in South Dakota ponds. North American Journal of Fisheries Management 13:134–140.

Taylor, J. F., A. C. Preston, D. Guy, and H. Migaud. 2011. Ploidy effects on hatchery survival, deformities, and performance in Atlantic Salmon (*Salmo salar*). Aquaculture 315:61–68.

Teskeredžić, E., E. M. Donaldson, Z. Teskeredžić, I. I. Solar, and E. McLean. 1993. Comparison of hydrostatic pressure and thermal shocks to induce triploidy in Coho Salmon (*Oncorhynchus kisutch*). Aquaculture 117:47–55.

Teuscher, D. M., D. J. Schill, D. J. Megargle, and J. C. Dillon. 2003. Relative survival and growth of triploid and diploid Rainbow Trout in two Idaho reservoirs. North American Journal of Fisheries Management 23:983–988.

Wagner, E. J., R. E. Arndt, M. D. Routledge, D. Latremouille, and R. F. Mellenthin. 2006. Comparison of hatchery performance, agnostic behavior, and poststocking survival between diploid and triploid Rainbow Trout of three different Utah strains. North American Journal of Aquaculture 68:63–73.

Walters, C. J., and J. R. Post. 1993. Density-dependent growth and competitive asymmetries in size-structured fish populations: a theoretical model and recommendations for field experiments. Transactions of the American Fisheries Society 122:34–45.

Warrillow, J. A., D. C. Josephson, W. D. Youngs, and C. C. Krueger. 1997. Differences in sexual maturity and fall emigration between diploid and triploid Brook Trout *Salvelinus fontinalis* in an Adirondack lake. Canadian Journal of Fisheries and Aquatic Sciences 54:1808–1812.

WGFD (Wyoming Game and Fish Department). 2002. Annual progress report for projects in the 2001 work schedule. WGFD, Cheyenne.

Withler, R. E., W. C. Clarke, J. Blackburn, and I. Baker. 1998. Effect of triploidy on growth and survival of pre-smolt and post-smolt Coho Salmon (*Oncorhynchus kisutch*). Aquaculture 168:413–422.

Yamamoto, A., and T. Iida. 1994. Oxygen consumption and hypoxic tolerance of triploid Rainbow Trout. Fish Pathology 29:245–251.

SUPPORTING INFORMATION

Additional supplemental material may be found online in the Supporting Information section at the end of the article.